



Phylogeny and new taxonomy of the Booted Eagles (Accipitriformes: Aquilinae)

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Abstract

We present a phylogeny of all booted eagles (38 extant and one extinct species) based on analysis of published sequences from seven loci. We find molecular support for five major clades within the booted eagles: *Nisaetus* (10 species), *Spizaetus* (4 species), *Clanga* (3 species), *Hieraaetus* (6 species) and *Aquila* (11 species), requiring generic changes for 14 taxa. Additionally, we recommend that the Long-crested Eagle (*Lophaetus occipitalis*) and the Black Eagle (*Ictinaetus malaiensis*) remain in their monotypic genera, due to their distinctive morphology. We apply the recently resurrected genus *Clanga* for the spotted eagles (previously *Aquila* spp.) to resolve the paraphyly of the genus *Aquila* such that the clade including the Booted Eagle (*H. pennatus*), Little Eagle (*H. morphnoides*), Pygmy Eagle (*H. weiskei*), Ayres's Eagle (*H. ayresii*) and Wahlberg's Eagle (*H. wahlbergi*) can remain in the genus *Hieraaetus*. The Rufous-bellied Eagle should be retained in the genus *Lophotriorchis*. For consistency in English names, we recommend that the term “hawk-eagles” be used only for the species in the genera *Nisaetus* and *Spizaetus*. We suggest following new or modified English names: Cassin's Eagle (*Aquila africana*), Bonaparte's Eagle (*A. spilogaster*), Ayres's Eagle (*Hieraaetus ayresii*), and Black-and-chestnut Hawk-Eagle (*Spizaetus isidori*).

Key words: Molecular phylogeny, morphology, *Nisaetus*, *Spizaetus*, *Clanga*, *Hieraaetus*, *Aquila*, *Oroaetus*, *Spizastur*, *Lophotriorchis*

Introduction

The booted eagles in the subfamily Aquilinae have fully feathered tarsi (i.e. boots) and belong to a monophyletic

group that is sister to harpy eagles (Harpiinae) and does not include sea eagles (Haliaeetinae), solitary eagles (Buteoninae) and snake eagles (Circaetinae) (Stresemann & Amadon 1979; Amadon 1982; Lerner & Mindell 2005). Although monophyly of the booted eagles is well supported by all recent molecular studies (Wink & Sauer-Gurth 2004; Lerner & Mindell 2005; Griffiths *et al.* 2007), there are still differing opinions about the taxonomic relationships within the group (Table 1) and several molecular studies have examined aspects of these relationships (Helbig *et al.* 2005; Gamauf *et al.* 2005 a, b; Lerner & Mindell 2005; Haring *et al.* 2007; Griffiths *et al.* 2007). Depending on the authority, there are 36 extant species of booted eagles (Dickinson & Remsen 2013) or 38 (Gill & Donsker 2016), and one recently extinct species, Haast's Eagle *Aquila moorei* (Haast, 1872), currently recognized in the genera: *Nisaetus*, *Stephanoaetus*, *Spizaetus*, *Hieraetus*, *Polemaetus*, *Lophaetus*, *Lophotriorchis*, *Ictinaetus*, *Clanga* and *Aquila*. Here, we shed light on the systematics of booted eagles presenting a phylogeny of all booted eagles based on analyses of published sequences from seven loci (Figure 1). Based on this, and previous published work, we also make taxonomic recommendations on their classification and nomenclature.

Methods

We obtained aquiline sequences from GenBank for all booted eagle taxa for two mitochondrial (mt) genes (cytochrome b [CYT-B] and NADH dehydrogenase subunit 2 [ND2]) and five nuclear (nuc) loci (recombination activating protein 1 [RAG-1], lactate dehydrogenase intron 3 [LDH], beta-fibrinogen gene intron 7 [B-FIB 7], adenylate kinase 1 exon 6 [AK], and myelocytomatosis viral oncogene-like protein gene exon 3 [MYC]). For each of these loci, datasets consisted of at least 19 taxa (Bunce *et al.* 2005; Helbig *et al.* 2005; Gamauf *et al.* 2005b; Lerner & Mindell 2005; Griffiths *et al.* 2007; Haring *et al.* 2007; Kocum *et al.* 2009). All other loci with booted eagle sequences in GenBank were excluded because they were present for only 1–3 taxa. When more than one individual had been sequenced for a locus, we chose the longest sequence for our dataset. In order to limit missing data, we did not include multiple individuals for each taxon even when multiple individuals had been sequenced for some loci (usually mt genes). We included only the individual with the longest available sequence or, in cases where two or more individuals were sequenced for the maximum length of the locus, we chose the individual with the smaller (i.e. earlier) submission number. We obtained sequences from 38 different extant species and one extinct species of booted eagle, and two outgroup species (Supplemental Table 1).

We created separate data sets for each individual locus and three concatenated datasets comprising: 1) both mt genes (2 loci, 41 taxa); 2) all nuc loci (5 loci, 28 taxa); and 3) all mt and nuc loci concatenated (7 loci, 41 taxa). These datasets contained differing numbers of taxa according to the number of available sequences for each locus. Additionally, we created four more datasets: (4) a dataset including only the taxa with sequences for all seven loci (n=16), (5) a dataset including taxa with five or more loci (n=26), (6) a dataset including taxa with two or more loci (n=36), and (7) a dataset including taxa with both mt genes (n=33). We concatenated datasets of multiple loci using Geneious v.6.1 (Biomatters) and BioEdit v7.2.0 (Ibis Biosciences). We calculated the GC content, % variable sites, and pairwise % identity in Geneious v.6.1. Parsimony informative sites were calculated using MEGA 5.1 (Tamura *et al.* 2011).

Sequences were aligned using Clustal-W (Thompson *et al.* 1994) in Geneious v.6.1 or BioEdit with default settings and manual adjustments. Partitions and corresponding evolutionary models were chosen using PartitionFinder (Lanfear *et al.* 2012).

We performed maximum likelihood analyses and bootstrapping in the RAxML blackbox web-server using the combined bootstrapping and ML search algorithm (Stamatakis *et al.* 2008). Bayesian analyses were performed in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) on the CIPRES Science Gateway (Miller *et al.* 2010) with four independent runs, each with four chains. We sampled from the chains every 500 generations for ten million generations, and assessed convergence of runs and parameter sampling using Tracer v1.5 (Rambaut & Drummond 2012). A burnin value of 200 (i.e. 100,000 generations) was chosen by identifying the plateau region of posterior probability distributions visualized in Tracer v1.5 (Rambaut & Drummond 2012). We viewed and formatted the trees using FigTree v1.4.0 (Rambaut 2012).

Post-burnin topologies from Bayesian analyses were visualized in DensiTree v 2.2.4. (Bouckaert 2014). The set of all post-burnin trees from both runs was reduced for viewing in DensiTree by creating a “consensus tree” using average branch lengths for each recovered topology and viewing all such consensus trees.

We consulted Dickinson *et al.* (2011) regarding uncertainties in dating of certain generic and species descriptions.

TABLE 1. Generic treatment of booted eagles varying in recent global taxonomic lists. Species whose genus did not vary among taxonomic lists are not shown (i.e. eight species of *Aquila*, Tawny Eagle, Steppe Eagle, Eastern Imperial Eagle, Spanish Imperial Eagle, Gurney's Eagle, Wedge-tailed Eagle, Golden Eagle, and Verreaux's Eagle; Booted Eagle, *Hieraetus*; Long-crested Eagle *Lophaeetus*, Black Eagle, *Ictinaetus*; Martial Eagle, *Polemaetus*; Black Hawk-Eagle, *Spizaetus*; Ornate Hawk-Eagle, *Spizaetus*). English names after Gill & Donsker [2016].

	Gill & Donsker 2016	GRIN 2016	Clements <i>et al.</i> 2014	Ferguson-Lees & Christie 2005	Dickinson & Remsen 2013	del Hoyo & Collar 2014
Cassin's Hawk-Eagle	<i>Aquila</i>	<i>Aquila</i>	<i>Aquila</i>	<i>Spizaetus</i>	<i>Aquila</i>	<i>Aquila</i>
Bonelli's Eagle	<i>Aquila</i>	<i>Aquila</i>	<i>Aquila</i>	<i>Hieraetus</i>	<i>Aquila</i>	<i>Aquila</i>
African Hawk-Eagle	<i>Aquila</i>	<i>Aquila</i>	<i>Aquila</i>	<i>Hieraetus</i>	<i>Aquila</i>	<i>Aquila</i>
Little Eagle	<i>Hieraetus</i>	<i>Aquila</i>	<i>Hieraetus</i>	<i>Hieraetus</i>	<i>Hieraetus</i>	<i>Hieraetus</i>
Pygmy Eagle	<i>Hieraetus</i>	<i>Aquila</i>	<i>Hieraetus</i>	<i>Hieraetus</i>	<i>Hieraetus</i>	<i>Hieraetus</i>
Wahlberg's Eagle	<i>Hieraetus</i>	<i>Aquila</i>	<i>Hieraetus</i>	<i>Hieraetus</i>	<i>Hieraetus</i>	<i>Hieraetus</i>
Ayres's Hawk-Eagle	<i>Hieraetus</i>	<i>Aquila</i>	<i>Hieraetus</i>	<i>Hieraetus</i>	<i>Hieraetus</i>	<i>Hieraetus</i>
Lesser Spotted Eagle	<i>Clanga</i>	<i>Lophaeetus</i>	<i>Clanga</i>	<i>Aquila</i>	<i>Clanga</i>	<i>Clanga</i>
Indian Spotted Eagle	<i>Clanga</i>	<i>Clanga</i>	<i>Clanga</i>	<i>Aquila</i>	<i>Clanga</i>	<i>Clanga</i>
Greater Spotted Eagle	<i>Clanga</i>	<i>Clanga</i>	<i>Clanga</i>	<i>Aquila</i>	<i>Clanga</i>	<i>Clanga</i>
Rufous-bellied Eagle	<i>Lophotriorchis</i>	<i>Lophotriorchis</i>	<i>Lophotriorchis</i>	<i>Hieraetus</i>	<i>Lophotriorchis</i>	<i>Lophotriorchis</i>
Black-and-white Hawk-Eagle	<i>Spizaetus</i>	<i>Spizaetus</i>	<i>Spizaetus</i>	<i>Spizaetus</i>	<i>Spizaetus</i>	<i>Spizaetus</i>
Black-and-chestnut Eagle	<i>Spizaetus</i>	<i>Spizaetus</i>	<i>Spizaetus</i>	<i>Oroaetus</i>	<i>Spizaetus</i>	<i>Spizaetus</i>
Changeable Hawk-Eagle	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Spizaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>
Flores Hawk-Eagle	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Spizaetus</i>	-	<i>Nisaetus</i>
Sulawesi Hawk-Eagle	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Spizaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>
Philippine Hawk-Eagle	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Spizaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>
Pinsker's Hawk-Eagle	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>	-	<i>Nisaetus</i>	<i>Nisaetus</i>
Wallace's Hawk-Eagle	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Spizaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>
Javan Hawk-Eagle	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Spizaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>
Blyth's Hawk-Eagle	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Spizaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>
Mountain Hawk-Eagle	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Spizaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>
Legge's Hawk-Eagle	<i>Nisaetus</i>	<i>Nisaetus</i>	<i>Nisaetus</i>	-	-	-

Results

The concatenated dataset was comprised of ~75% nuc sequences (five loci, 6,086 bp, Table 2) and ~25% mt sequences (two genes, 2,184 bps). In terms of variability, more than six times as many parsimony-informative sites were found in mt genes (87%) as compared to nuc loci (13%).

TABLE 2. DNA sequence availability, variability, and length for loci and combined datasets.

	# taxa	# bps	informa- tive indels	GC content	# variable sites	% variable sites	# parsimony informative sites	% parsimony informative sites	pairwise % identity
Mitochondrial									
CYT-B	41	1143	0	0.485	460	40.2	381	33.3	91.2
ND2	33	1041	0	0.478	470	45.2	330	31.7	87.3
All Mitochondrial	41	2184	0		930	42.6	711	32.6	
Nuclear									
RAG-1	28	2872	0	0.441	130	4.5	42	1.5	99.3
LDH	26	553	2	0.346	94	10.1	18	3.3	98.2
B-FIB 7	19	1040	0	0.361	111	10.6	16	1.5	98.5
AK	26	549	2	0.600	88	16.4	19	3.5	96.4
MYC	23	1072	0	0.488	24	2.2	11	1.0	99.5
All Nuclear	28	6086	4		447	7.3	106	1.7	
All Sites	41	8270	4		1377	20.2	817	9.9	

Three separate partitions by codon position were supported by PartitionFinder analyses for mt loci. These partitions were employed for Bayesian analyses of mt data. The best supported models for each locus were the general time reversible with a gamma distributed rate variation among sites and a proportion of invariant sites (i.e. GTR + I + G, first and third mitochondrial codon positions), Hasegawa-Kishino-Yano (i.e. HKY for B-FIB 7, HKY + G for LDH, HKY + I for AK and RAG-1, and HKY + I + G for second mitochondrial codon positions), and Kimura 2-parameter (i.e. K80, MYC). The average standard deviation of split frequencies for the 41 taxon dataset was 0.001889 and ESS values of the combined four runs exceeded 10,000 for all parameters.

Phylogenetic trees for each of the seven loci individually and the seven concatenated datasets described above were compared to identify any differences in topology from each other and from published trees. Trees for CYT-B, RAG-1, and MYC are included in the supplemental information (Figures S1–3) as they included larger taxon sets than in previous publications; trees for ND2, LDH, B-FIB 7 and AK are not shown, as they were topologically identical to previously published trees (Lerner & Mindell 2005; Helbig *et al.* 2005).

The phylogenetic placement for *Aquila adalberti* C. L. Brehm, 1861 differed significantly between the analyses of CYT-B (sister taxon to *A. heliaca* Savigny, 1809, the taxon of which it was previously treated as a sub-species) and RAG-1 (diverging directly after a clade containing *Nisaetus* and *Stephanoaetus*, and sister to all other booted eagles). Because the RAG-1 sequence for *A. adalberti* (EU345533.1) was not from a peer-reviewed publication and its validity could not be confirmed, we excluded it from further analyses of concatenated datasets. Informative indels present in two loci (AK and LDH) are mapped on the phylogenetic tree containing all taxa (Figure 1), though not all taxa in the dataset were sequenced for AK and LDH (see Table 2 and Supplemental Table 1). Topologies did not differ substantially among concatenated datasets, so only the three most taxon-inclusive datasets are shown here (Figures 1 and 2). The Bayesian consensus tree from a dataset including all taxa (n=41) and all loci is shown in Figure 1 with both bootstrap values and Bayesian posterior probabilities. All Bayesian consensus topologies (described above) for the dataset of all nuc loci (n=28 taxa) and for the dataset of mt genes (n=41) are shown in Figure 2 as DensiTree cloudograms. Alignments for each of these three datasets have been deposited at Data Dryad (doi:10.5061/dryad.q10q6).

All analyses and datasets supported three monophyletic genera: *Nisaetus*, *Spizaetus* and *Clanga*. Support values from the mt analysis and the all-loci analysis for these genera were high: *Nisaetus* (Bayesian posterior probability [bpp] 1, bootstrap value [bv] 93–100), *Spizaetus* (bpp 1, bv 97–100), and *Clanga* (bpp 0.96–1, bv 96–99; Table 3). Monophyly of *Hieraaetus sensu stricto* was supported by analyses of the mt data (bpp 1, bv 84) and the full dataset (bpp 1, bv 99), as well as with the Bayesian analyses of the nuc dataset (bpp 1), but not with the maximum likelihood analysis of the nuc data (bv 63). Monophyly of the genus *Aquila* and relationships among taxa within the genus were not well-supported by any dataset or analysis. The highest support for monophyly of *Aquila* was with the maximum likelihood analysis of the full dataset (bv 77).

TABLE 3. Nodal support values for genera from mitochondrial data (MT), nuclear loci (NUC) and all seven loci (ALL LOCI) from maximum likelihood (ML) and Bayesian (Bayes) analyses.

	MT		NUC		ALL LOCI	
	ML	Bayes	ML	Bayes	ML	Bayes
<i>Nisaetus</i>	93	1	100	1	99	1
<i>Spizaetus</i>	97	1	100	1	100	1
<i>Lophotriorchis</i>	83	0.99	n/a	n/a	86	1
<i>Clanga</i>	97	0.96	99	1	96	0.99
<i>Hieraaetus</i> + <i>Aquila</i>	57	0.92	82	1	95	1
<i>Hieraaetus</i>	84	1	63	1	99	1
<i>Aquila</i>	62	0.65	0	0	77	0.73

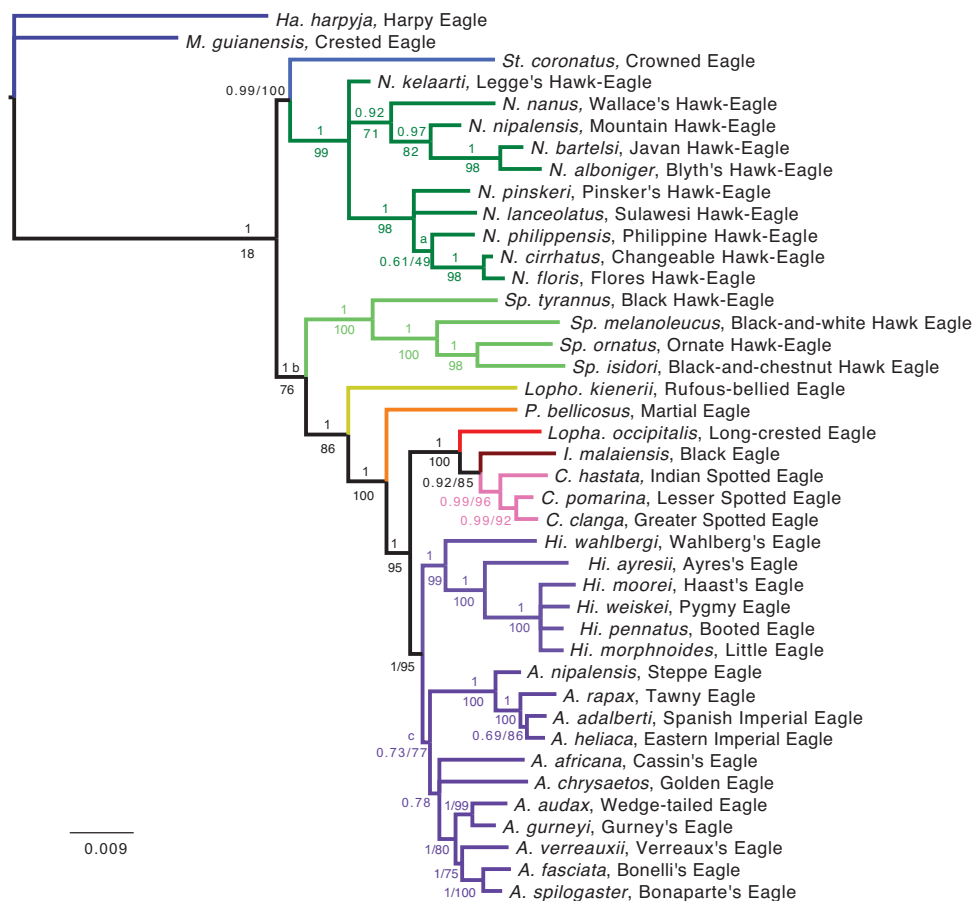


FIGURE 1. Bayesian Consensus Tree of the 7-locus dataset for 39 taxa of booted eagles and two outgroups. Bayesian posterior probabilities for each node are shown above the line adjacent to the corresponding node, bootstrap values are below the line or after the '/'. Supporting indels of 5 bp, and 17 bp and two indels of 4 bp in length, indicated by a, b and c, respectively, are mapped on the tree.

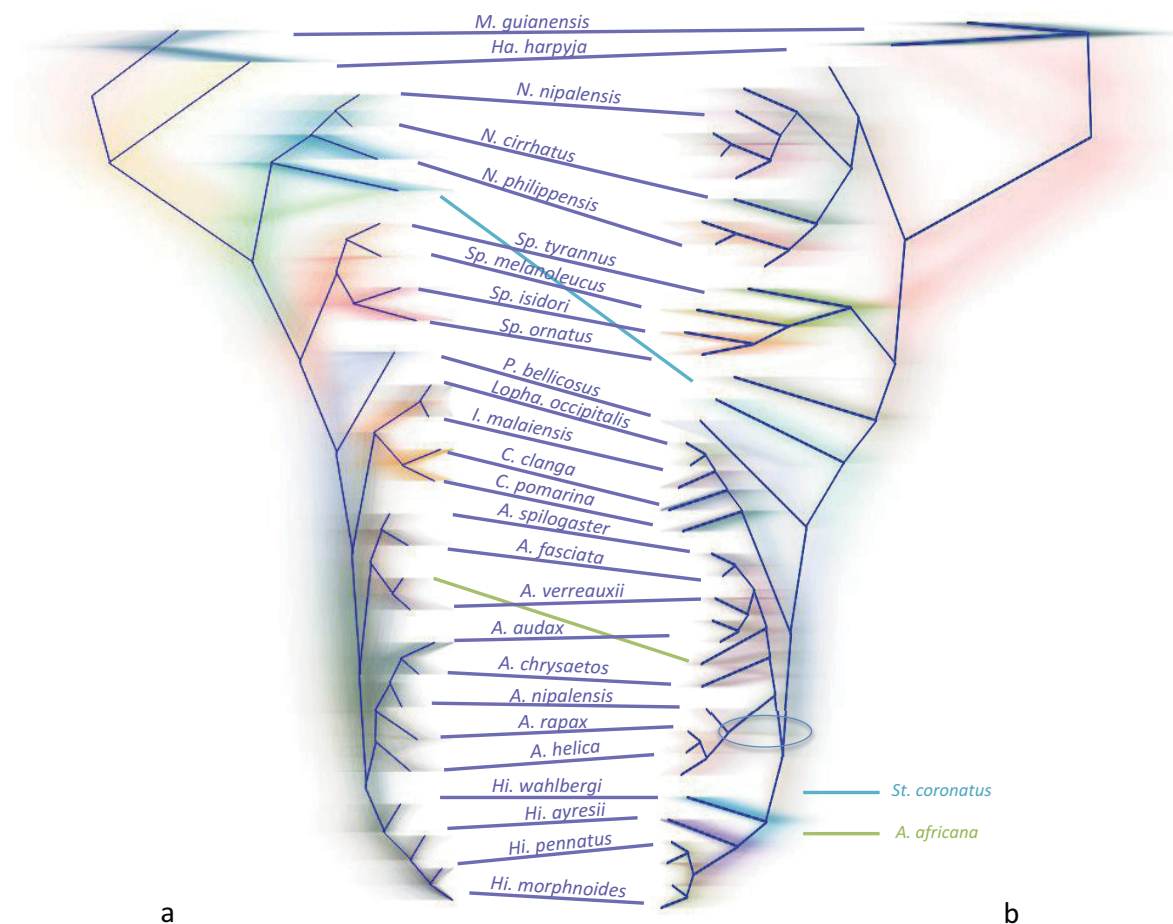


FIGURE 2. All Bayesian Consensus topologies from (a) five nuclear loci (n=28 taxa) and (b) two mitochondrial genes (n=41 taxa) visualized in DensiTree v 2.2.4. Taxa with close relationships share similar branch coloration. The circled green branch denotes an alternate topology in which the clade containing *A. nipalensis* is sister to the clade containing the genus *Hieraaetus*, rendering the genus *Aquila* polyphyletic.

Discussion

Our analyses agree with other published works in recovering *Aquila*, *Hieraaetus* and *Spizaetus* as polyphyletic genera, so we revised the generic names using their phylogenetic placement in this study, previous molecular and morphological work, and previous taxonomic suggestions (Table 1). Figures shown here use the revised taxonomy described below.

Crowned Eagle. The placement of the Crowned Eagle *Stephanoaetus coronatus* (Linnaeus, 1766) differs among previous studies and among our datasets and methods of analysis. Lerner & Mindell (2005) found that this species was the earliest diverging species after the divergence of the Asian and New World hawk-eagles, while Helbig *et al.* (2005) and Griffiths *et al.* (2007) found support for a sister relationship between the Crowned Eagle and the Asian hawk-eagles. Haring *et al.* (2007), however, did not find a close relationship between the Crowned Eagle and the Asian hawk-eagles. This difference in placement persists in our separate analyses of nuc and mt data. Using nuc data alone (Figure 2a, data from Lerner & Mindell 2005; Helbig *et al.* 2005; and Kocum *et al.* 2009), the Crowned Eagle either falls within the early diverging clade of Asian hawk-eagles (most probable topology in Figure 2a) or is the earliest diverging booted eagle. With only mt data, it diverges after both clades of Asian and New World hawk-eagles (CYT-B data from Helbig *et al.* 2005 and nd2 data from Lerner & Mindell 2005). The combined nuc and mt dataset supports it as the earliest diverging taxon in the large *Nisaetus* hawk-eagle clade with strong bootstrap support (bv 100) but with low Bayesian support (bpp 0.69), which is consistent with Griffiths *et al.* (2007). We recommend retaining *Stephanoaetus* W.L. Sclater, 1922: p. 75 as a monotypic genus given its long branch length, lack of close relatives and persistent phylogenetic uncertainty.

Structurally, *Stephanoaetus* is characterized by a short, narrow cranium; relatively short, rounded wings and long, broad tail; narrow trunk; short, robust tarsometatarsi with the highest degree of torsion of any booted eagle; and the most massive toes and talons of any booted eagle (Parry 2001). Adults are barred below, with a full, divided crest; immatures have a white head and underparts. The species is specialized to hunt medium-sized forest mammals. It is highly vocal, giving long rising and falling series of loud, short clear, rather deep musical notes (c. AV# 10646, <http://avocet.zoology.msu.edu/recordings/10646>) in flight.

Hawk-eagles. The hawk-eagles form two separate clades: one in the New World [*Spizaetus* Vieillot, 1816a: p. 24, for which *S. ornatus* (Daudin, 1800) is the type by subsequent designation (G.R. Gray, 1840), bpp 1.00, bv 100] and one in Asia [*Nisaetus* Hodgson, 1836: 228, for which *N. nipalensis* Hodgson, 1836 is the type by original designation: bpp 1.00, bv 99]. These two clades have been recovered in other molecular studies (Gamauf *et al.* 2005a; Helbig *et al.* 2005; Lerner & Mindell 2005; Haring *et al.* 2007; Griffiths *et al.* 2007). The taxa in these clades share relatively short primaries, long tails, elongate tarsi, and usually long crests, traits which are convergent adaptations to rainforest habitats. The New World hawk-eagles [Black Hawk-Eagle *Spizaetus tyrannus* (zu Wied-Neuwied, 1820), Ornate Hawk-Eagle *S. ornatus*, Black-and-chestnut Hawk-Eagle *Oroaetus isidori* (Des Murs, 1845) and Black-and-white Hawk-Eagle *Spizastur melanoleucus* (Vieillot, 1816b)] are closely related and should be placed in the genus *Spizaetus* Vieillot, 1816a (Remsen *et al.* 2015, Table 1 and references therein). Their tarsi are robust relative to most Asian hawk-eagles (Parry 2001). They have striking color patterns that differ greatly between species. The Neotropical hawk-eagles we treat within *Spizaetus* all give loud, shrill, clear short whistles, which may be delivered in series (see recordings of each at xeno-canto.org or the Macaulay Library at the Cornell Lab of Ornithology macaulaylibrary.org).

The dissimilarity of *Spizaetus africanus* (Cassin, 1865), *S. ornatus* and *S. tyrannus* from other taxa then placed within *Spizaetus* was recognized by Jollie (1977) based on morphological analysis. In fact, W. L. Sclater erected the genus *Cassinaetus* Sclater, 1919 for the former species. Brown & Amadon (1968) also stated that *Spizaetus africanus*, *S. ornatus* and *S. tyrannus* are not obviously closely related to any of the other species placed in the genus *Spizaetus* at that time, but they did not draw further taxonomic conclusions. As shown in Figures 1 and 2, we support the inclusion of the taxa previously placed in the genera *Spizastur* and *Oroaetus* as members of the genus *Spizaetus*, and *Cassinaetus* as a member of the genus *Aquila*.

The ten Asian hawk-eagles form a strongly-supported clade and we support their assignment to the genus *Nisaetus* (Haring *et al.* 2007; Dickinson & Remsen 2013; Clements *et al.* 2014; Table 1). Although structurally similar to *Spizaetus* species, most species have a more gracile tarsometatarsus (Parry 2001), and they are much more uniform in plumage, adults typically being more or less uniform brown above and barred below. All members are highly vocal, giving thin shrill, relatively high-pitched whistles (see recordings at online call libraries cited above); at least some species have two major song types including both a complex rather rapid series and a shorter, slower series (Rasmussen & Anderton 2012). Within the Asian hawk-eagle clade we find support for sister relationships between Changeable Hawk-Eagle *Nisaetus cirrhatus* (J.F. Gmelin, 1788) and Flores Hawk-Eagle *N. floris* (E. Hartert, 1898), and between Javan Hawk-Eagle *N. bartelsi* (Stresemann, 1924) and Blyth's Hawk-Eagle *N. alboniger* Blyth, 1845. Placement of Legge's Hawk-Eagle *Nisaetus kelaarti* (Legge, 1878) within the larger *Nisaetus* clade is unresolved. It is however, well-supported as a separate species from *N. nipalensis* (Gjershaug *et al.* 2008) and is treated as such in Gill & Donsker (2016).

Ferguson-Lees & Christie (2005) treated the Changeable Hawk-Eagle *Nisaetus limnaeetus* (Horsfield, 1821), Andaman Hawk-Eagle *N. andamanensis* (Tytler, 1865) and Simeuluë Hawk-Eagle *N. vanheurni* (Junge, 1936) as distinct species, while Rasmussen & Anderton (2012) and Clements *et al.* (2014) considered *N. limnaeetus* as a full species, with *N. andamanensis* and by implication *N. vanheurni* as subspecies of *N. limnaeetus*. Furthermore, Dickinson & Remsen (2013) combined them all under *N. cirrhatus* following the treatment recommended by Gamauf *et al.* (2005b) that did not support their recognition as separate species. There was not enough existing sequence data (i.e. <300 bps mt DNA) to fully evaluate their species status in this study.

Flores Hawk-Eagle *Nisaetus floris* has been considered a separate species from *N. cirrhatus* (Gjershaug *et al.* 2004; del Hoyo & Collar 2014; Gill & Donsker 2016), and the two are recovered as closely related sister taxa in this study. Similarly, Legge's Hawk-Eagle (*N. kelaarti*) has been treated as a separate species from *N. nipalensis* based on morphological, plumage, vocal and genetic traits (Gjershaug *et al.* 2008; Rasmussen & Anderton 2012; Gill & Donsker 2016). In all our trees, these were recovered as non-sister taxa, supporting their recognition as separate species. Based on molecular evidence, Gamauf *et al.* (2005a,b) recommended treating the Pinsker's

Hawk-Eagle *Nisaetus pinskeri* (Preleuthner & Gamauf, 1998) as a separate species from the Philippine Hawk-Eagle *N. philippensis* (Gould, 1863). The genetic divergence between these two taxa is 3.4% in CYT-B. Preleuthner & Gamauf (1998) showed earlier that there are distinct structural and plumage pattern differences between these two taxa.

The name “hawk-eagle” has been used for small eagles with a relatively long tail in the genera *Spizaetus* and *Nisaetus*. It is, however, also currently used for several other less closely related eagles, including the African Hawk-Eagle *Aquila spilogaster* (Bonaparte, 1850), Cassin’s Hawk-Eagle *A. africana*, and Ayres’s Hawk-Eagle *Hieraaetus ayresii* (J.H. Gurney, 1862). We suggest that the English group name for these eagles should be changed from Hawk-Eagle to Eagle, as has already been done for the latter but not the former two species in Dickinson & Remsen (2013). Additionally, we suggest that the name African Hawk-Eagle be changed to Bonaparte’s Eagle, honoring Charles Lucien Bonaparte (the nephew of Emperor Napoleon), and describer of the species in 1850. Ayres’s Eagle was previously suggested for *H. ayresii* by Clark (2012). For consistency with other members of its genus, we suggest altering the English name Black-and-chestnut Eagle *Spizaetus isidori* to Black-and-chestnut Hawk-Eagle (Table 4).

Rufous-bellied Eagle. The Rufous-bellied Eagle has, until recently, been recognized by most sources as *H. kienerii* (de Sparre, 1835), a member of the genus *Hieraaetus* Kaup, 1844, of which the type species is the Booted Eagle *H. pennatus* (J. F. Gmelin, 1788). Lerner & Mindell (2005) and Haring *et al.* (2007) found that this species was not closely related to the other members of *Hieraaetus*. Haring *et al.* (2007) proposed to treat it as a separate genus, resurrecting for it the name *Lophotriorchis* Sharpe, 1874, of which it is the type species, and we apply that name here. Both mt loci were available for this taxon, though no nuc data were found in GenBank at the time of our analysis. In our analyses, it is not closely related to *Stephanoaetus*, *Nisaetus*, or *Spizaetus*, but is more closely related to the clades comprising *Polemaetus*, *Lophaetus*, *Ictinaetus*, *Clanga*, *Hieraaetus* and *Aquila*. The adult plumage of *Lophotriorchis* is uniquely blackish above with white throat and chestnut lower underparts, while immatures are white below. This genus has unusually long toes and tarsi, and is a specialized bird predator, capturing them by stooping (Brown & Amadon 1968; Parry 2001). Its vocalizations are series of high, shrill, staccato notes punctuated by slightly longer, plaintive shrill slurred notes (Rasmussen & Anderton 2012; <http://www.xeno-canto.org/22445>).

Martial Eagle. The Martial Eagle *Polemaetus bellicosus* (Daudin, 1800), with its distinct morphology, has long been recognized in the monotypic genus *Polemaetus* Heine, 1890. Its placement as sister to the clade containing *Lophaetus*, *Ictinaetus*, *Clanga*, *Hieraaetus* and *Aquila* is strongly supported here (bv 100, bpp 1.0), as in other molecular studies (Lerner & Mindell 2005; Helbig *et al.* 2005).

This very large savannah eagle is characterized by unusually long, gracile tarsi, perhaps an adaptation to tall grass and/or dangerous large reptilian prey (Parry 2001). It also has an unusually high wing loading with deep wing slots, presumably for fast gliding over its huge territory (Parry 2001). Adults are dark gray above with dark-speckled white underparts. Vocalizations include a very loud, robust series of short staccato notes (e.g., ML 20449; <http://macaulaylibrary.org/audio/20449>).

Clanga, Ictinaetus and Lophaetus. A well-supported clade includes the Black Eagle *Ictinaetus malaiensis* (Temminck, 1822) the Long-crested Eagle *Lophaetus occipitalis* (Daudin, 1800) and the three species of spotted eagles: Greater Spotted Eagle *Clanga clanga* (Pallas, 1811), Lesser Spotted Eagle *C. pomarina* (C. L. Brehm, 1831), and Indian Spotted Eagle *C. hastata* (Lesson, 1831a) (bv 100, bpp 1.0 this study; Lerner & Mindell 2005). Helbig *et al.* (2005) and Wink & Sauer-Gürth (2004) also recovered a clade including the Long-crested Eagle and the spotted eagles. The inclusion of the Black Eagle in this clade was further supported by Griffiths *et al.* (2007). There is currently much confusion about the taxonomy of these species, though morphological and genetic evidence support the species status of *C. pomarina* and *C. hastata* (Parry *et al.* 2002; Väli 2006).

Helbig *et al.* (2005) suggested including *Aquila clanga* and *A. pomarina* in the genus *Lophaetus* together with *L. occipitalis*. However, as *Ictinaetus malaiensis* also belongs to this clade (Figure 1), the correct genus name for this clade would be *Ictinaetus* Blyth, 1843, which has priority over *Lophaetus* Kaup, 1847. Nevertheless, we recommend keeping the Black Eagle (*Ictinaetus malaiensis*) and the Long-crested Eagle (*Lophaetus occipitalis*) in their own genera, as these two eagle species are strikingly different in morphology both from each other as well as from the other species in the clade (Figure 1).

TABLE 4. Proposed taxonomy of booted eagles (subfamily Aquilinae) based on the data and analyses presented here, Gamauf *et al.* [2005a, b], Haring *et al.* [2007], Helbig *et al.* [2005], Bunce *et al.* [2005] and Lerner & Mindell [2005]. English names after Gill & Donsker [2016]. Our suggested new English names in bold.

<u>Genus <i>Aquila</i> Brisson, 1760</u>	
Tawny Eagle	<i>Aquila rapax</i> (Temminck, 1828)
Steppe Eagle	<i>Aquila nipalensis</i> Hodgson, 1833
Eastern Imperial Eagle	<i>Aquila heliaca</i> Savigny, 1809
Spanish Imperial Eagle	<i>Aquila adalberti</i> C.L. Brehm, 1861
Gurney's Eagle	<i>Aquila gurneyi</i> G.R. Gray, 1861
Wedge-tailed Eagle	<i>Aquila audax</i> (Latham, 1801)
Golden Eagle	<i>Aquila chrysaetos</i> (Linnaeus, 1758)
Cassin's Eagle	<i>Aquila africana</i> (Cassin, 1865)
Verreaux's Eagle	<i>Aquila verreauxii</i> Lesson, 1831
Bonelli's Eagle	<i>Aquila fasciata</i> Vieillot, 1822
Bonaparte's Eagle	<i>Aquila spilogaster</i> (Bonaparte, 1850)
<u>Genus <i>Hieraaetus</i> Kaup, 1844</u>	
Booted Eagle	<i>Hieraaetus pennatus</i> (Gmelin, 1788)
Little Eagle	<i>Hieraaetus morphnoides</i> (Gould, 1841)
Pygmy Eagle	<i>Hieraaetus weiskei</i> (Reichenow, 1900)
Wahlberg's Eagle	<i>Hieraaetus wahlbergi</i> (Sundevall, 1850)
Ayres's Eagle	<i>Hieraaetus ayresii</i> (Gurney, 1862)
Haast's Eagle (extinct)	<i>Aquila moorei</i> (Haast, 1872)
<u>Genus <i>Lophaetus</i> Kaup, 1847</u>	
Long-crested Eagle	<i>Lophaetus occipitalis</i> (Daudin, 1800)
<u>Genus <i>Ictinaetus</i> Blyth, 1843</u>	
Black Eagle	<i>Ictinaetus malaiensis</i> (Temminck, 1822)
Lesser Spotted Eagle	<i>Clanga pomarina</i> (C.L. Brehm, 1831)
Indian Spotted Eagle	<i>Clanga hastata</i> (Lesson, 1831)
Greater Spotted Eagle	<i>Clanga clanga</i> (Pallas, 1811)
<u>Genus <i>Polemaetus</i> Heine, 1890</u>	
Martial Eagle	<i>Polemaetus bellicosus</i> (Daudin, 1800)
<u>Genus <i>Lophotriorchis</i> Sharpe, 1874</u>	
Rufous-bellied Eagle	<i>Lophotriorchis kienerii</i> (de Sparre, 1835)
<u>Genus <i>Stephanoaetus</i> W.L. Sclater, 1922</u>	
Crowned Eagle	<i>Stephanoaetus coronatus</i> (Linnaeus, 1766)
<u>Genus <i>Spizaetus</i> Vieillot, 1816a</u>	
Black Hawk-Eagle	<i>Spizaetus tyrannus</i> (zu Wied-Neuwied, 1820)*
Ornate Hawk-Eagle	<i>Spizaetus ornatus</i> (Daudin, 1800)
Black-and-white Hawk-Eagle	<i>Spizaetus melanoleucus</i> (Vieillot, 1816b)
Black-and-chestnut Hawk-Eagle	<i>Spizaetus isidori</i> (Des Murs, 1845)
<u>Genus <i>Nisaetus</i> Hodgson, 1836</u>	
Changeable Hawk-Eagle	<i>Nisaetus cirrhatus</i> (Gmelin, 1788)
Flores Hawk-Eagle	<i>Nisaetus floris</i> (Hartert, 1898)
Sulawesi Hawk-Eagle	<i>Nisaetus lanceolatus</i> (Temminck & Schlegel, 1844)
Philippine Hawk-Eagle	<i>Nisaetus philippensis</i> (Gould, 1863)
Pinsker's Hawk-Eagle	<i>Nisaetus pinskeri</i> (Preleuthner & Gamauf, 1998)
Wallace's Hawk-Eagle	<i>Nisaetus nanus</i> (Wallace, 1868)
Javan Hawk-Eagle	<i>Nisaetus bartelsi</i> (Stresemann, 1924)
Blyth's Hawk-Eagle	<i>Nisaetus alboniger</i> Blyth, 1845
Mountain Hawk-Eagle	<i>Nisaetus nipalensis</i> Hodgson, 1836
Legge's Hawk-Eagle	<i>Nisaetus kelaarti</i> (Legge, 1878)

*Original description is on p. 357, not p. 360 as stated in Peters (1931), Stresemann & Amadon (1979), and AOU (1998).

The Long-crested Eagle is substantially smaller than the other eagles in this clade (50–56cm, versus 65–80cm for the Black Eagle and 55–71cm for the genus *Clanga*), and has a long, broad cranium, bowed jugal bars and mandibular rami; elongate, gracile tarsometatarsi; short, broad primaries and a very short tail compared to other booted eagles (Brown & Amadon 1968; Ferguson-Lees & Christie 2001; Parry 2001). Its vocalizations include a nasal yapping series and prolonged squealing notes (<http://www.xeno-canto.org/268791>).

The Black Eagle has a variety of unique morphological traits, such as its extraordinarily broad and long wings, which have the deepest wing slots of any booted eagle, and its long, broad tail; these characteristics give it very low wing loading and allow it to cruise very slowly just over the canopy (Ferguson-Lees & Christie 2005). *Ictinaetus* is also characterized by a shallow bill and a very broad gape, and a short tarsometatarsus and lateral digits, but very long, relatively straight claws, presumably adaptations for snatching nestlings and eating them unplucked in flight (Parry 2001). Adults are black, while immatures have some buff in plumage, the amount differing racially. Black Eagles vocalize sporadically (P.C.R. pers. obs.), giving a slow series of short hoarse modulated whistles (<http://www.xeno-canto.org/65517>).

The new genus *Aquiloides* Wells & Inskipp, 2012 was proposed for the spotted eagles, but Gregory & Dickinson (2012) showed that *Clanga* Adamowicz, 1858 has priority over *Aquiloides*, so we follow the latter authors, thereby avoiding paraphyly in *Aquila*. The spotted eagles in the genus *Clanga* are mid-sized eagles with broad, rounded wings, shortish, rounded tails, and round nares. The secondaries of adults are longer than in juveniles, unlike *Aquila* in which the reverse is true (Wells & Inskipp 2012). They have large gapes but smaller, shorter bills than in *Aquila*, and the crania are long and broad; their tarsi are long but their feet are small (Parry 2001). Adults are uniform brown, and immatures have white-spotted upperwing coverts. Spotted eagles primarily give short, sharp yelping calls in series (Rasmussen & Anderton 2012).

***Hieraaetus* and *Aquila*.** This large clade uniting eagles in the genera *Hieraaetus* Kaup, 1844 *sensu stricto* and *Aquila* Brisson, 1760, of which the Golden Eagle *A. chrysaetos* (Linnaeus, 1758) is the type by tautonymy, has strong support (bpp 1, bv 95). The genus *Hieraaetus* forms a clade with strong support here (bpp 1, bv 99) and in other studies (Wink & Sauer-Gürth 2004; Helbig *et al.* 2005; Lerner & Mindell 2005). Bonelli's Eagle *Aquila fasciata* Vieillot, 1822 and Bonaparte's Eagle (*A. spilogaster*) were previously recognized as members of the genus *Hieraaetus* (Table 1), but have since been shown to be nested within the genus *Aquila* (Figures 1 and 2), and are sister to Verreaux's Eagle *A. verreauxii* Lesson, 1831b (bpp 0.68, bv 80; Wink & Sauer-Gürth 2004; Helbig *et al.* 2005; Lerner & Mindell 2005; Haring *et al.* 2007). Trainor *et al.* (2013) found no diagnostic DNA markers distinguishing *Aquila f. fasciata* from *A. f. renschi* (Stresemann, 1932), and more genetic variation within *A. f. fasciata* than between the two subspecies. This does not support the proposal by Thiollay (1994) and Ferguson-Lees & Christie (2001) that *A. f. renschi* should be accorded full species status. There was insufficient published sequence data to test this proposal with our analyses.

Although the Pygmy Eagle *Hieraaetus weiskei* (Reichenow, 1900) was long treated as a subspecies of the Little Eagle *H. morphnoides* (Gould, 1841), it should be considered a distinct species based on DNA sequence divergence (Bunce *et al.* 2005; Lerner & Mindell 2005) and morphology (Parry 2001; Gjershaug *et al.* 2009).

There is low statistical support for the clade recognized here as *Aquila* (Table 3; bpp 0.73, bv 77), although an indel of two bps is unique to all eagles in the genus *Aquila* shown in Figure 1 with the possible exception of *A. africana*, *A. gurneyi* G.R. Gray, 1861 and *A. adalberti*, which were not sequenced for this locus. There is essentially a four-way polytomy within the genus *Aquila*, among (1) the clade containing *A. nipalensis* Hodgson, 1833, *A. rapax* (Temminck, 1828), *A. adalberti* and *A. heliaca*, (2) *A. africana*, (3) *A. chrysaetos*, and (4) the clade containing *A. audax* (Latham, 1801), *A. gurneyi*, *A. verreauxii*, *A. fasciata* and *A. spilogaster*. The well-supported clade uniting the genus *Hieraaetus* is sister to this polytomy, and given the low support for the *Aquila* clade, is best considered a fifth branch of the unresolved polytomy.

The visualization in Figure 2 provides further insight into the phylogenetic uncertainty among eagles in the genera *Hieraaetus* and *Aquila*. Both the nuc data (Figure 2a) and the mt data (Figure 2b) show that there are multiple alternate topologies for the branching order among the *Aquila* eagles. Alternative topologies are shown as additional lines. Most importantly, both datasets show large uncertainty as to whether the clade containing *A. spilogaster*, *A. fasciata*, *A. verreauxii* and *A. audax* is sister to or diverges prior to the clade containing *A. nipalensis*, *A. rapax*, and *A. heliaca*. If the latter is the true species phylogeny, then *Hieraaetus* would be nested within *Aquila*, bearing a sister relationship with the clade containing *A. nipalensis*.

In both datasets, the placement of the Golden Eagle (*A. chrysaetos*) within the clade of *Hieraaetus* and *Aquila*

is uncertain; it is not clear if it has a closer relationship with the clade containing *A. nipalensis*, *A. rapax*, and *A. heliaca* (most probable topology in Figure 2a), or with the clade containing *A. spilogaster*, *A. fasciata*, *A. verreauxii* and *A. audax* (most probable topology in Figure 2b), or if it diverged before either of these two clades (secondary topology in Figure 2b).

The question needs to be asked if *Aquila* and *Hieraaetus* should be combined as a single genus or whether *Aquila* should be split into further genera. Wolters (1975–1982), for example, recognized the following additional genera *Eutolmaetus* Blyth, 1844 for *A. fasciata* and *A. spilogaster* and *Cassinaetus* Selater, 1922 for *A. africana*. Although these genera do not conflict with the phylogenies of the current study, their recognition does not solve the broader issue of a lack of statistical support for the *Aquila* clade as it currently stands, nor would it solve the potential paraphyly of the genus *Aquila*. We suggest that further molecular studies should focus on this issue.

Wink & Sauer-Gürth (2004) proposed that the genus *Hieraaetus* should be included within the genus *Aquila*, as earlier suggested by Dementiev *et al.* (1966). Helbig *et al.* (2005) included only *Hieraaetus fasciatus* and *H. spilogaster* in *Aquila*, and retained the genus *Hieraaetus* for *H. pennatus*, *H. morphnoides*, *H. ayresii* and *H. wahlbergi* (Sundevall, 1850). They argued that there was moderate molecular support for the monophyly of the small-bodied *Hieraaetus* species, and that they share two potential phenotypic synapomorphies: (1) dimorphic adult plumage and (2) vocalizations of high-pitched, drawn-out whistles, without the repetitive “clucking, barking, and yelping” territorial calls typical of *Aquila* species. Debus *et al.* (2007) presented behavioral, vocal and morphological support for treating *Hieraaetus* and *Aquila* as separate genera. Clark (2012) also argued for maintaining *Hieraaetus* and *Aquila* as distinct genera.

Cassin’s Eagle (*Aquila africana*) of Central and West Africa has until recently been recognized as a member of the genus *Spizaetus*. Lerner & Mindell (2005) and Haring *et al.* (2007) found, using mt DNA, that this species was closely related to *Aquila* species. Haring *et al.* (2007) proposed that it should be included in that genus, a change that is reflected in many recent taxonomic treatments (see Table 1) and in our figures. Our analyses of the two mt genes and a newly sequenced nuc locus (MYC) supports the placement of Cassin’s Eagle as a member of the genus *Aquila*. Using nuc data alone (Figure 2a) *Aquila africana* is sister to *Aquila verreauxii* (bpp 1.00; bootstrap 91). With mt data, the placement of *A. africana* is either within the same clade as that containing *A. verreauxii*, as the earliest divergence; it diverges after the divergence of *A. chrysaetos* within that clade; or it diverges before that clade diverges (Figure 2b). Resolving the placements of Cassin’s Eagle and the Golden Eagle remains a priority. Ferguson-Lees & Christie (2005) treat the Indian Tawny Eagle as a distinct species, *Aquila vindhiana* Franklin, 1831, but this has not been adopted by other works (e.g. Rasmussen & Anderton 2012; Dickinson & Remsen 2013). We regard it as a subspecies of *Aquila rapax* because of its minimal plumage and genetic differences (100% genetic similarity with *A. rapax* in Africa in 264 bp CYT-B sequence; JOG unpubl. data).

The expanded genus *Aquila* is not readily characterized either in plumage, structure, or osteologically (Parry 2001), especially now that it includes some species formerly in *Hieraaetus*. Further study is required, but it appears that the species remaining in *Hieraaetus* can be characterized by relatively short, narrow crania, shallow bills, short robust tarsometatarsi, and rather short tails (Parry 2001), as well as dimorphic adult plumage and high-pitched, prolonged whistles, unlike the clucking, barking, or yelping series typical of *Aquila* species (Helbig *et al.* 2005; Debus *et al.* 2007; Clark 2012).

Conclusion

In conclusion, our phylogeny of booted eagles shows molecular support for five major genera: *Nisaetus* (10 species), *Spizaetus* (4), *Clanga* (3), *Hieraaetus* (6) and *Aquila* (11). In implementing the changes based on this finding, we support generic changes for 14 taxa as outlined above and implemented in Figures 1 and 2.

Future work should address (1) the differing phylogenetic placement of the Crowned Eagle (*Stephanoetus coronatus*) with nuclear versus mitochondrial data; (2) the species status of the Changeable Hawk-Eagle (*Nisaetus limnaetus*), the Andaman Hawk-Eagle (*Nisaetus andamanensis*) and the Simeuluë Hawk-Eagle (*Nisaetus vanheurni*) using sequence data from multiple nuclear loci and a larger amount of mitochondrial data; and (3) the relationships within the genus *Aquila*, especially the placement of Cassin’s Eagle (*A. africana*) and the Golden Eagle (*A. chrysaetos*).

Acknowledgements

Some previously unpublished data used in this manuscript were collected by Meade Krosby, Chris Huddleston, Mike Braun, and Wallace Holznagel. Had they lived, Andreas Helbig (deceased 2005) and Wallace Holznagel (deceased 2009) would certainly have been invited to be co-authors on this manuscript. This project was made possible by the work of many, including researchers who collected and deposited specimens and DNA sequences; curators and collection managers who cared for the specimens and DNA data; software developers (cited within); the support staff of GenBank; and, recordists who contributed to the online bird vocalization databases xeno-canto (<http://www.xeno-canto.org/>), AVoCet (<http://avocet.zoology.msu.edu/>), and the Macaulay Library (<http://macaulaylibrary.org/>). Two anonymous reviewers provided feedback that greatly improved the manuscript. The Ford/Knight Collaborative Research Fund and the Joseph Moore Museum James Cope Fund at Earlham College provided financial support for Sonia Kabra, Rachel Wadleigh, and Heather Lerner. The National Science Foundation provided enhanced network infrastructure that was used during molecular analyses (Award #1440689).

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SUPPLEMENTAL TABLE 1. GenBank Sequences and references.

IOC Name	GenBank Organismal Name	Locus Name		ND2	RAG-1	LDH	B-FIB 7	AK	MYC
		CYT-B							
<i>Harpia harpyja</i>	<i>Harpia harpyja</i>	AJ604495 ⁵	AY987090 ⁷	EF078735 ³	AJ601509 ⁵	AY987188 ⁷	AJ601480 ⁵		GU189444 ⁶
<i>Morphnus guianensis</i>	<i>Morphnus guianensis</i>	AJ604496 ⁵	AY987088 ⁷	EF078748 ³	AJ601510 ⁵	AY987187 ⁷	AJ601481 ⁵		GU189445 ⁶
<i>Aquila rapax</i>	<i>Aquila rapax</i>	AJ604491.1 ⁵	AY987104.1 ⁷	AJ601447.1 ⁵	AJ601505.1 ⁵	AY987197.1 ⁷	AJ601476.1 ⁵		GU189450.1 ⁶
<i>Aquila nipalensis</i>	<i>Aquila nipalensis</i>	AJ604489.1 ⁵	AY987108.1 ⁷	AJ601445.1 ⁵	AJ601503.1 ⁵	AY987199.1 ⁷	AJ601474.1 ⁵		GU189449.1 ⁶
<i>Aquila heliaca</i>	<i>Aquila heliaca</i>	AJ604488.1 ⁵	AY987106.1 ⁷	AJ601444.1 ⁵	AJ601502.1 ⁵	AY987198.1 ⁷	AJ601473.1 ⁵		GU189448.1 ⁶
<i>Aquila chrysaetos</i>	<i>Aquila chrysaetos</i>	AJ604486.1 ⁵	AY987116.1 ⁷	AJ601442.1 ⁵	AJ601499.1 ⁵	AY987203.1 ⁷	AJ601470.1 ⁵		GU189447.1 ⁶
<i>Aquila verreauxii</i>	<i>Aquila verreauxii</i>	AJ604492.1 ⁵	AY987123.1 ⁷	AJ601448.1 ⁵	AJ601506.1 ⁵	AY987206.1 ⁷	AJ601477.1 ⁵		GU189451.1 ⁶
<i>Hieraetus pennatus</i>	<i>Hieraetus pennatus</i>	AJ604500.1 ⁵	AY987110.1 ⁷	AJ601456.1 ⁵	AJ601514.1 ⁵	AY987200.1 ⁷	AJ601485.1 ⁵		GU189457.1 ⁶
<i>Hieraetus morphnoides</i>	<i>Hieraetus morphnoides</i>	AJ604499.1 ⁵	AY987112.1 ⁷	AJ601455.1 ⁵	AJ601513.1 ⁵	AY987201.1 ⁷	AJ601484.1 ⁵		GU189456.1 ⁶
<i>Hieraetus wahlbergi</i>	<i>Hieraetus wahlbergi</i>	AJ604493.1 ⁵	AY987115.1 ⁷	AJ601449.1 ⁵	AJ601507.1 ⁵	AY987202.1 ⁷	AJ601478.1 ⁵		GU189458.1 ⁶
<i>Lophaetus occipitalis</i>	<i>Lophaetus occipitalis</i>	AJ604502.1 ⁵	AY987103.1 ⁷	AJ601458.1 ⁵	AJ601516.1 ⁵	AY987196.1 ⁷	AJ601487.1 ⁵		GU189453.1 ⁶
<i>Stephanoaetus coronatus</i>	<i>Stephanoaetus coronatus</i>	AJ604511.1 ⁵	AY987100.1 ⁷	AJ601467.1 ⁵	AJ601525.1 ⁵	AY987194.1 ⁷	AJ601496.2 ⁵		GU189462.1 ⁶
<i>Spizaetus tyrannus</i>	<i>Spizaetus tyrannus</i>	AJ604510.2 ⁵	AY987096.1 ⁷	AJ601466.1 ⁵	AJ601524.1 ⁵	AY987190.1 ⁷	AJ601495.1 ⁵		GU189461.1 ⁶
<i>Spizaetus ornatus</i>	<i>Spizaetus ornatus</i>	AJ604508.2 ⁵	AY987098.1 ⁷	AJ601464.1 ⁵	AJ601522.1 ⁵	AY987192.1 ⁷	AJ601493.1 ⁵		GU189460.1 ⁶
<i>Spizaetus melanoleucus</i>	<i>Spizaetus melanoleucus</i>	AJ604505.1 ⁵	AY987097.1 ⁷	AJ601461.1 ⁵	AJ601519.1 ⁵	AY987191.1 ⁷	AJ601490.1 ⁵		GU189459.1 ⁶
<i>Nisaeetus nipalensis</i>	<i>Nisaeetus nipalensis</i>	AJ604507.1 ⁵	AY987094.1 ⁷	AJ601463.1 ⁵	AJ601521.1 ⁵	AY987189.1 ⁷	AJ601492.1 ⁵		GU189464.1 ⁶
<i>Polemaetus bellicosus</i>	<i>Polemaetus bellicosus</i>	AJ604504.1 ⁵	AY987102.1 ⁷	AJ601460.1 ⁵	AJ601518.1 ⁵	AY987195.1 ⁷	AJ601489.1 ⁵		
<i>Spizaetus isidori</i>	<i>Oroaetus isidori</i>	AJ812238.1 ⁵	AY987099.1 ⁷	AJ812239.1 ⁵	AJ812241.1 ⁵	AY987193.1 ⁷	AJ812240.1 ⁵		
<i>Aquila spilogaster</i>	<i>Hieraetus spilogaster</i>	AJ604501.1 ⁵	AY987122.1 ⁷	AJ601457.2 ⁵	AJ601515.1 ⁵	AY987205.1 ⁷	AJ601486.1 ⁵		
<i>Hieraetus ayresii</i>	<i>Hieraetus ayresii</i>	AJ604497.1 ⁵	AY987114.1 ⁷	AJ601453.1 ⁵	AJ601511.1 ⁵		AJ601482.1 ⁵		GU189454.1 ⁶
<i>Aquila audax</i>	<i>Aquila audax</i>	AJ604484.1 ⁵	AY987124.1 ⁷	AJ601441.1 ⁵	AJ601498.1 ⁵		AJ601469.1 ⁵		GU189446.1 ⁶
<i>Nisaeetus cirrhatus</i>	<i>Spizaetus cirrhatus</i>	AJ604506.2 ⁵	AY987092.1 ⁷	AJ601462.1 ⁵	AJ601520.1 ⁵		AJ601491.1 ⁵		GU189463.1 ⁶
<i>Aquila fasciata</i>	<i>Hieraetus fasciatus</i>	AJ604498.1 ⁵	AY987119 ⁷	AJ601454.1 ⁵	AJ601512.1 ⁵		AJ601483.1 ⁵		GU189455.1 ⁶

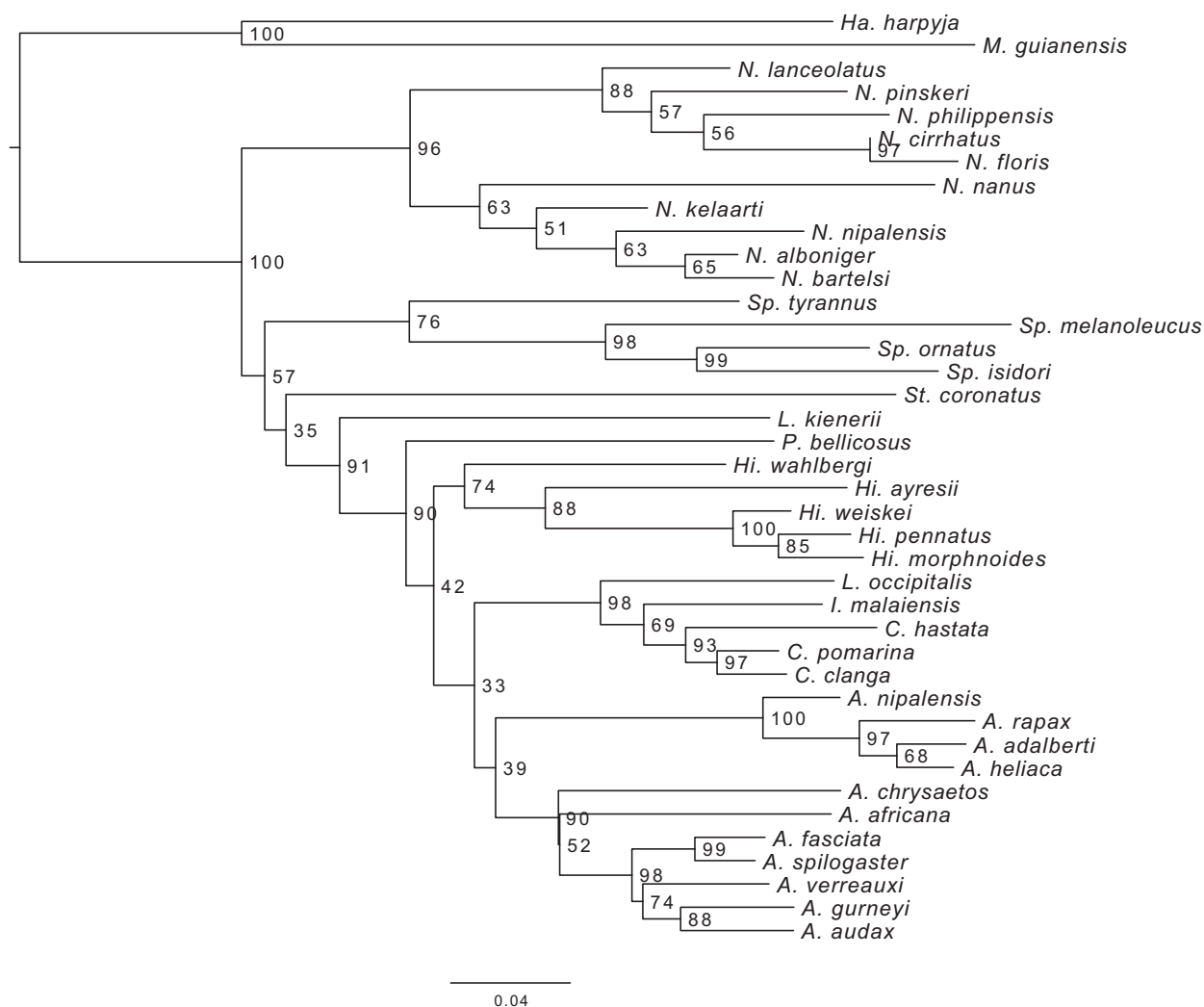
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SUPPLEMENTAL TABLE 1. (Continued)

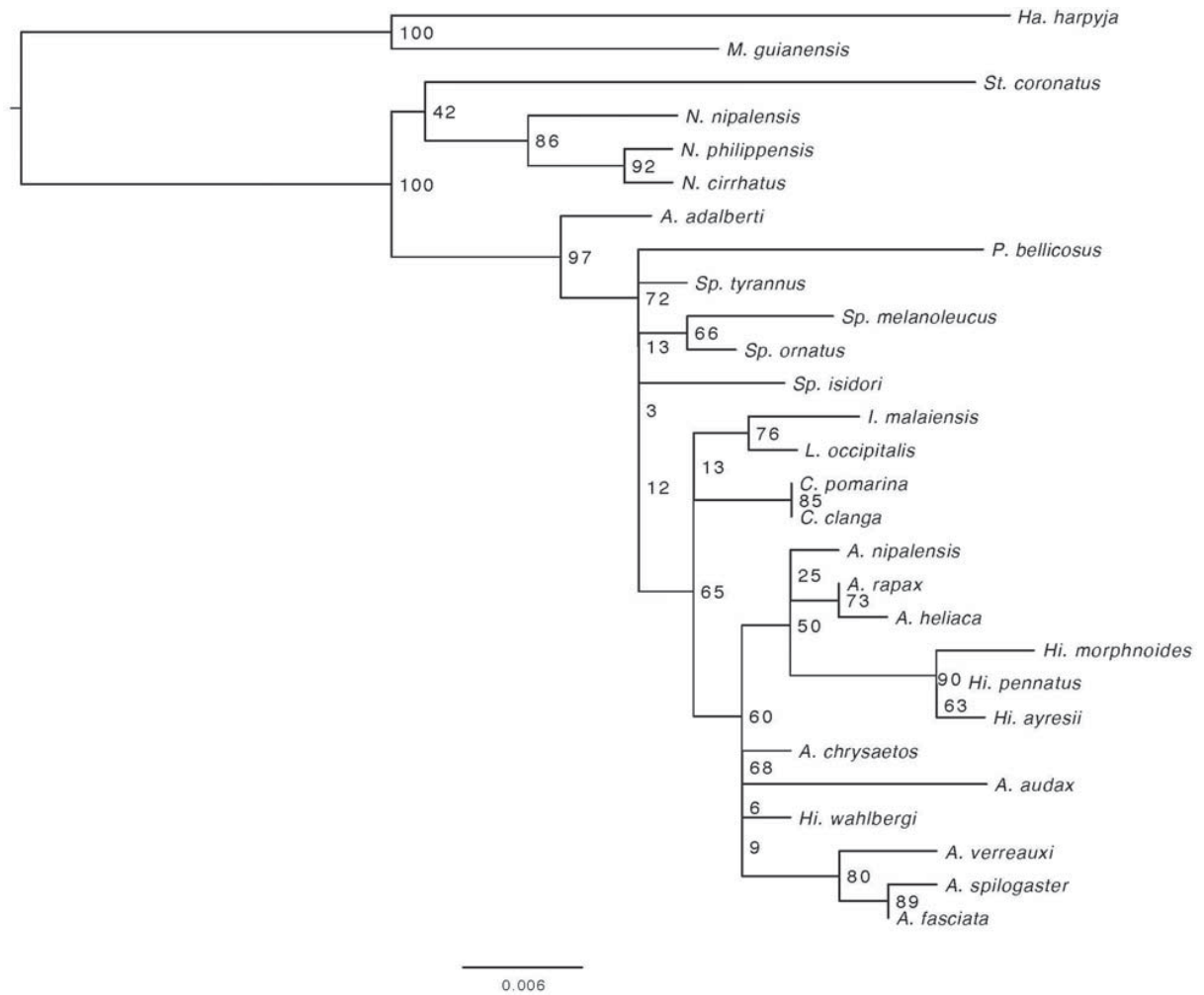
IOC Name	GenBank Organismal Name	Locus Name		ND2	RAG-1	LDH	B-FIB 7	AK	MYC
		CYT-B							
<i>Clanga clanga</i>	<i>Aquila clanga</i>	AJ60487 ⁵		AY987105 ⁷	AJ601443 ⁵	AJ601501 ⁵		AJ601472 ⁵	
<i>Clanga pomarina</i>	<i>Aquila pomarina</i>	AJ604490.1 ⁵			AJ601446.1 ⁵	AJ601504.1 ⁵		AJ601475.1 ⁵	GU189452.1 ⁶
<i>Nisaetus philippensis</i>	<i>Spizaetus philippensis</i>	AJ604509.2 ⁴			AJ601465.2 ⁵	AJ601523.1 ⁵		AJ601494.1 ⁵	
<i>Ictinaetus malaiensis</i>	<i>Ictinaetus malayensis</i>	AY754056.1 ¹		AY987109.1 ⁷	EF078739.1 ³				
<i>Aquila africana</i>	<i>Spizaetus africanus</i>	AY987295.1 ⁷		AY987117.1 ⁷					GU189451.1 ⁶
<i>Lophotriorchis kienerii</i>	<i>Hieraetus kienerii</i>	AY754054.1 ¹		AY987101.1 ⁷					
<i>Clanga hastata</i>	<i>Aquila hastata</i>	AY987286.1 ⁷		AY987107.1 ⁷					
<i>Hieraetus weiskei</i>	<i>Hieraetus weiskei</i>	AY987291.1 ⁷		AY987113.1 ⁷					
<i>Nisaetus lanceolatus</i>	<i>Spizaetus lanceolatus</i>	AY701129.1 ⁴		AY987091.1 ⁷					
<i>Nisaetus namus</i>	<i>Nisaetus namus</i>	AY987273.1 ⁷		AY987093.1 ⁷					
<i>Nisaetus alboniger</i>	<i>Nisaetus alboniger</i>	AY987275.1 ⁷		AY987095.1 ⁷					
<i>Aquila gurneyi</i>	<i>Aquila gurneyi</i>	AY987303.1 ⁷		AY987125.1 ⁷					
n/a	<i>Aquila adalberti</i>	Z73463.1 ⁵			EU345533.1 ^{8*}				
<i>Nisaetus floris</i>	<i>Nisaetus floris</i>	AY701118.1 ²							
<i>Nisaetus bartelsi</i>	<i>Nisaetus bartelsi</i>	EF459658.1 ⁴							
<i>Nisaetus kelaarti</i>	<i>Nisaetus kelaarti</i>	EF459647.1 ⁴							
<i>Nisaetus pinskeri</i>	<i>Spizaetus pinskeri</i>	AY701125.1 ⁴							
n/a	<i>Harpagornis moorei</i>	AY754047.1 ¹							
# taxa (inc. 2 outgroups)		41	33	28	26	19	26	23	

Key:

¹Bunce *et al.* 2005; ²Gamauf *et al.* 2005a; ³Griffiths *et al.* 2007; ⁴Haring *et al.* 2007; ⁵Helbig *et al.* 2005; ⁶Kocum *et al.* 2009; ⁷Lerner & Mindell 2005; ^{8*}omitted from analysis (see details in text)



SUPPLEMENTAL FIGURE 1. Maximum Likelihood Analysis of CYT-B sequences.



SUPPLEMENTAL FIGURE 2. Maximum Likelihood Analysis of RAG-1 sequences.



SUPPLEMENTAL FIGURE 3. Cladogram from Maximum Likelihood Analysis of MYC sequences.